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Schafstall, Nick

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Changes in species composition and diversity of a montane beetle community over the last millennium in the High Tatras, Slovakia: implications for forest conservation and management

Nick Schafstall[1*], Nicki Whitehouse[2,3], Niina Kuosmanen[1,4], Helena Svobodová- Svitavská [5], Mélanie Saulnier[1], Richard Chiverrell[6], Peter Fleischer[7,8], Petr Kuneš[9], Jennifer Clear[10]

1. Dept. of forest ecology, Czech University of Life Sciences, Kamycka 129, 165 00 Praha-Suchdol, Czechia; nick.schafstall@gmail.com; kuosmanen.niina@gmail.com; melanie.saulnier14@gmail.com

2. Dept. Of Archaeology, School of Humanities, University of Glasgow, 1 University Gardens, Glasgow G12 8QQ, United Kingdom; nicki.whitehouse@glasgow.ac.uk

3. School of Geography, Earth and Environmental Sciences, Plymouth University, Drake Circus, Plymouth, Devon, PL4 8AA, United Kingdom

4. Department of Geosciences and Geography, Faculty of Science, P.O. Box 64 (Gustaf Hällströmin katu 2) FI-00014 University of Helsinki, Finland

5. Laboratory of paleoecology, Institute of Botany, Czech Academy of Sciences, Zámek 1, 252 43 Průhonice , Czechia; helena.svitavska@ibot.cas.cz

6. Dept. of Geography and Planning, University of Liverpool, Roxby Building, Liverpool, L69 7ZT, United Kingdom R.C.Chiverrell@liverpool.ac.uk

7. Faculty of Forestry, Technical University in Zvolen, Ul. T. G. Masaryka 24, 960 01 Zvolen, Slovakia p.fleischersr@gmail.com

8. State Forest of TANAP, Tatranská Lomnica 64, 059 60 Vysoké Tatry-Tatranská Lomnica, Slovakia

9. Dept. of Botany, Charles University, Benátská 433/2, 128 01 Praha 2, Czechia petr.kunes@natur.cuni.cz

10. Dept. of Geography, Hope University, Hope Park, Liverpool L16 9JD, United Kingdom clearj@hope.ac.uk

* Corresponding author email:

nick.schafstall@gmail.com

Abstract

Montane biomes are niche environments high in biodiversity with a variety of habitats. Often isolated, these non-continuous remnant ecosystems inhabit narrow ecological zones putting them under threat from changing climatic conditions and anthropogenic pressure. Twelve sediment cores were retrieved from a peat bog in Tatra National Park, Slovakia, and correlated to each other by wiggle-matching geochemical signals derived from micro-XRF scanning, to make a reconstruction of past conditions. A fossil beetle (Coleoptera) record, covering the last 1000 years at 50- to 100-year resolution, gives a new insight into changing flora and fauna in this region. Our findings reveal a diverse beetle community with varied ecological groups inhabiting a range of forest, meadow and synanthropic habitats. Changes in the beetle community were related to changes in the landscape, driven by anthropogenic activities. The first clear evidence for human activity in the area occurs c. 1250 CE and coincides with the arrival of beetle species living on the dung of domesticated animals (e.g. *Aphodius* spp.). From 1500 CE, human (re)settlement, and activities such as pasturing and charcoal burning, appear to have had a pronounced effect on the beetle community. Local beetle diversity declined steadily towards the present day, likely due to an infilling of the forest hollow leading to a decrease in moisture level. We conclude that beetle communities are directly affected by anthropogenic intensity and land use change. When aiming to preserve or restore natural forest conditions, recording their past changes in diversity can help guide conservation and restoration. In doing so, it is important to look back beyond the time of significant human impact, and for this, information contained in paleoecological records is irreplaceable.

Key words: Coleoptera; nature conservation; biodiversity; human impact; Central Europe; climate change.

1. Introduction

Montane biomes are diverse multi-functional environments with a variety of habitats often occupied by specific, endemic animal and plant communities constrained by environmental conditions (Kessler and Kluge, 2008; Dimitrov et al., 2012; Amori et al., 2019). Humans have progressively modified these ecosystems by altering land-use to their requirements, resulting in the decline of many plant and animal species. The establishment of national parks during the 20th century serves to preserve the remaining biodiversity in remote mountain areas, yet these montane forests are increasingly impacted by extreme climate events and their ecosystems are changing rapidly (McCain and Colwell, 2011; Elsen and Tingly, 2015). In particular, the frequency of extreme events disturbing forest ecosystems, such as drought and windstorms, have increased significantly in Europe and North America during the last 50 years (Schelhaas et al., 2003; Allen et al., 2010). However, historical recordings of disturbance agents are rare in some regions (Schelhaas et al., 2003). Paleoecological reconstructions can be used to understand the long-term effects of changing climate and anthropogenic pressure on the landscape structure and the flora and fauna in montane regions (La Sorte and Jetz, 2010; McCain and Colwell, 2011). In the last decades it has become apparent that linking paleoecology with conservation management is key to understand the effects of current conservation efforts (Froyd and Willis, 2008). Ecological data on longer time scales allow for a better reconstruction of natural variability in a landscape and give clearer results about ecological thresholds and resilience within a natural system. Furthermore, by addressing ecological data on longer time scales it can be argued if the current disturbance events in montane forests are unprecedented (Froyd and Willis, 2008; Kidwell, 2015).

Fossil pollen and botanical macrofossils are the most commonly used proxies for reconstructing paleoenvironment and vegetation structure (e.g. Magyari et al., 2012). Subfossil beetle (Coleoptera) remains are a valuable additional proxy to pollen as these can often be identified to species level and provide detailed information about past beetle habitats (e.g. van Geel et al., 1989). Many beetle species live in specific niche environments

because of their preferences for certain temperature and moisture levels, landscape openness and host plants (Elias, 2010). Local communities (< 400 m; Smith et al., 2010) are the source area for beetle remains at fossil sites. In previous studies, the comparison of fossil beetle assemblages with modern beetle communities provided valuable information about the timing and drivers of local beetle taxa extinctions (e.g. Whitehouse, 2006). Therefore, fossil beetle records provide not only detailed information to reconstruct landscape composition through time, but also contribute to solve issues in conservation and management (e.g. Buckland and Kenward, 1973; Gustavsson et al., 2009). Lindbladh et al. (2013) highlight fossil beetle remains as an underused, yet valuable proxy in forested landscape reconstructions as fossil beetles can contribute to the reconstruction of forest composition, (relative) amounts of old trees and coarse woody debris, and to reconstruct natural disturbances. Even insect outbreaks could potentially be quantified from fossil beetle remains.

Central Europe has a diverse landscape with high flora and fauna species diversity, and is currently under pressure from intensive land use (Turnock, 2002). The High Tatra Mountains are located on the border between Slovakia and Poland and are part of the Western Carpathian range, the highest range of the Carpathian Mountains. The area is a prominent UNESCO biosphere reserve with species such as brown bear (*Ursus arctos*), Eurasian lynx (*Lynx lynx*) and wolf (*Canis lupus*), and many endemic plant and animal species (unesco.org). In the last decades, extreme events such as windthrows and droughts have increased significantly in this region (e.g. Fleischer et al., 2017). Consequently, the Tatra Mountains are an ideal region to investigate long-term (millennial) changes in the local flora and fauna, based on pollen and beetle remains. In this study, we aim to 1) Reconstruct changes in diversity of the local forest beetle community and 2) Identify the drivers behind changes in beetle community and vegetation diversity. Understanding the drivers behind species composition and diversity change over the last 1000 years can be used as a

potential analogue to help understand the response and resilience of these ecosystems to future climate and anthropogenic changes.

2. Methods

2.1 Site area

Diera Hollow is a small forest hollow of 30 m x 80 m in size and located at 982 m a.s.l. on a former end moraine of the High Tatra Mountains near the village Tatranská Lomnica, Slovakia (49.09885° N, 20.15814° E; Figure 1). The region has a sub-continental climate with an average minimum temperature of -5.3 °C and an average maximum temperature of 15.4 °C. The mean annual rainfall is 830 mm (Tatranská Lomnica weather station, 830 m a.s.l.). Forest hollows are waterlogged anoxic peat depressions within a forest canopy. Due to their small to moderate size (~100 – 2000 m^2) their sediments reflect a local environmental signal. The pollen signal is representative of the vegetation recorded within a radius approximately 100 m of the site (Overballe-Petersen and Bradshaw, 2011), and comparable to the source area radius of 400 m for beetle remains (Smith et al., 2010). The site was heavily damaged by the autumnal storm Alžbeta in 2004 and is currently surrounded by pine (*Pinus*), spruce (*Picea abies*), larch (*Larix decidua*), birch (*Betula*) and bilberry (*Vaccinium myrtillus*). Seedlings of birch, bedstraw (*Galium* sp.), rosebay willowherb (*Epilobium angustifolium*) and sedges (*Carex* spp.) are present at the site. Prior to the windstorm in 2004, the area surrounding the study site was densely forested, with spruce as the dominant species.

2.2 Field methods

A master sediment core was extracted from Diera Hollow in 2016, with a 5 x 50 cm D-section corer (Jowsey, 1965; Aaby and Digerfeldt, 1986). To provide the volumes of material required for analysis of fossil beetles, a further 12 proximal sediment cores were sampled in 2017 using a gridded system, with a 10 x 50 cm D-section corer. To minimize the disturbance of the sampling site inside the nature reserve, sampling was performed by

collecting multiple parallel cores instead of digging trenches, a sampling method often used in paleoentomological studies (e.g. Forbes et al., 2020). Cores measured between 50 cm and 78 cm in total length due to variable moraine deposits and bedrock. The master core (88 cm in length) was radiocarbon dated and analyzed for geochemistry (Energy-Dispersive X-Ray Fluorescence: ED-XRF), subfossil beetles and pollen, while the additional cores were analyzed for beetle remains.

2.3 Chronology, geochemistry and core correlation

Four botanical macrofossil samples from the master core were dated in the Poznan radiocarbon laboratory (see supplementary data Table S1) and were used to establish a site chronology. The ^{14}C ages were calibrated with the IntCal13 curve (Reimer et al., 2013) within a Bayesian age-depth modelling routine 'BACON' (Blaauw and Christen, 2011), which modelled all age information, including the sediment surface, using a Student-t distribution that accounted for scatter and allowed statistical outliers (Figure 2). The Bayesian analysis (Christen and Perez, 2009) partitioned the core into three sections (31.3 cm thick) estimating the accumulation rate for each segment using a Markov Chain Monte Carlo (MCMC) approach. The modelling was constrained by a prior model of sediment accumulation rate.

All 13 cores, including the master profile, were analyzed for geochemistry on a wet-sediment basis using an Olympus Delta Professional ED-XRF mounted on the University of Liverpool Geotek Multi-Sensor Core Logger (MSCL). XRF core scanning is a non-destructive, rapid approach for quantifying elemental concentrations in a sediment core (Croudace et al., 2006) and has been used frequently in paleolimnological studies (Davies et al., 2015) and, to lesser extent, studies on peat cores (Poto et al., 2015; Longman et al., 2019). Patterns in geochemistry were comparable between the master profile and the 12 proximal cores; patterns in concentration of the atmospheric fallout pollutant Pb (Renburg et al., 2000) displayed a strongly repeatable signal. Profiles for conservative lithogenic elements, e.g. Rb, also showed strongly repeatable stratigraphic records. The strong

matches between the cores (Figures S1 – S4) facilitated the transfer of the age-depth model between cores and provided a basis for subsampling the 12 cores. These cores were pooled into 18 samples with total volumes 400 – 1600 ml, with narrower 1 – 4 cm intervals to provide greater detail for the last 100 years (400 – 500 ml) and the remainder in 4 – 7 cm depth intervals (800 – 1600 ml). Details on the subsampling can be found in figure S4.

2.4 Fossil beetle analysis

Fossil beetle preparation of the 18 samples followed the methods described in detail by Elias (2010). Samples were wet sieved at 250 µm and the organic remains were soaked in paraffin oil and floated in water. Isolated floats were sieved and rinsed before being stored in ethanol (C_2H_5OH). Beetle remains were picked under a binocular light microscope with 10x magnification and were identified to family, genus and species level with the use of online databases (Kerbtier.de, Cassidae.uni.wroc.pl) and museum collections in United Kingdom (Plymouth City Museum and Oxford Museum of National History) and Czechia (Czech National Museum in Prague, Regional Museum Roztoky u Prahy and the Moravian Museum in Brno). The minimum number of individuals (MNI) was calculated by adding up all elytra, heads and dorsal plates(pronota) identified as Coleoptera.

2.5 Ecological attributes

Specific ecological attributes of beetle genera and species were derived from literature through online databases; BugsCEP (Buckland and Buckland, 2006) and Biomap (2019), which contained full species descriptions. According to their ecological preferences, species or genera were divided into 20 functional groups to facilitate interpretation. Functional groups are personal interpretations used to summarize the ecology of beetle taxa and can vary to certain degree according to the type of study they are used for (e.g. archaeological vs. paleoecological). The functional groups in this study are based on previous work from the United Kingdom (e.g. Whitehouse, 2004). Many beetle species can be found in more than one type of landscape, and the ecology of taxa is as well often

197 constrained by their feeding strategies. Unless beetle taxa were clearly eurytopic, the most
198 dominant ecological feature was chosen for each beetle taxon: Eurytopic (appearing in a
199 wide variety of biotopes); Aquatic (living at least partially in water bodies); Aquatic standing
200 water (living in stagnant bodies of water); Aquatic running water (living in flowing water
201 bodies); Marsh/wetland (hygrophilous species living in marshes or wetlands); Bank
202 vegetation (living on vegetation at the banks of water bodies); Hygrophilous (living in a
203 variety of biotopes, with a high humidity as common factor); Heathland/moorland (living in
204 moderately wet, open landscape); Meadow (living in open landscape, often feeding on
205 meadow vegetation); Disturbed/arable (living on disturbed soils, often disturbed by
206 anthropogenic activities); Foul/dung (living in dung and rotting vegetation or other materials);
207 Dung (only living in dung); Dry decomposer (fungivore in dry environments); Wet
208 decomposer (mostly fungivores; found in moist places); Shaded woodland (living in shaded
209 woodland but in the understory); Trees (living on trees); Deciduous trees (living on
210 deciduous trees); Coniferous trees (living on coniferous trees); Deadwood (living in dying
211 trees and decaying wood) and Conifer pest (colonizing healthy trees).The category Conifer
212 pest was added as large quantities of conifer bark beetles (Curculionidae: Scolytinae) were
213 found and these could provide additional information about past disturbances. Beetle data
214 was displayed using the program Tilia (Grimm, 1990), zonation was performed by D-chord
215 cluster analysis (see section 2.7).
216
217 *2.6 Pollen analysis*
218 Pollen analysis of the 2016 master core was performed in continuous 1 cm resolution
219 between 1 – 70 cm and in 2 cm interval for the rest of the core, amounting to a total of 78
220 samples. Subsamples of 0.5 cm^3 were prepared with standard procedures of KOH-,
221 acetolysis- and HF-treatment (Fægri and Iversen, 1989). The samples were mounted in
222 glycerine and a minimum of 500 terrestrial pollen grains were identified under a light
223 microscope using a 400x magnification. Pollen identification was based on standard pollen
224 keys (Punt 1976, 2003; Beug, 2004), microtopographic atlases (Reille, 1992 – 1998), and a

reference collection in the Institute of Botany, CAS, Průhonice. Pollen data was plotted using the program C2 (Juggins, 2003). The full pollen dataset can be accessed upon personal request to the authors and will be published elsewhere.

2.7 Statistical analysis

Shannon's diversity index (Shannon and Weaver, 1949) takes both the number of individuals and the number of taxa into account, by calculating the natural log from the proportion of an individual species of the total sum of individuals. This diversity index is used commonly in ecology as well as archeology and paleoecology (Pielou, 1967; Liu et al., 2015). Both beetle diversity and pollen diversity were plotted against time to compare forest beetle community dynamics with forest vegetation dynamics.

To emphasize changes in the terrestrial beetle community, aquatic species were excluded from the following analyses; 266 out of 313 taxa remained. Raw counts were converted to percentages to account for differences in total sum of individuals per sample (Legendre and Legendre, 2012). The square-chord method (Overpeck et al., 1985) was used to calculate dissimilarities between all samples. A hierarchical cluster analysis was then performed on the resulting square-chord dissimilarity (SQD) matrix to identify patterns in the beetle assemblages. Ward's minimum variance criterion (Ward, 1963) was used to implement the hierarchical clustering, to define beetle zones. This technique produces compact, equal-sized dendrograms by minimizing the total within-cluster variance (Mirkin, 2005). Furthermore, a PCA (Gabriel, 1971) was performed on the samples according to their dissimilarity matrix, to explore which components (species) attributed most to the variance throughout the section. All statistical analyses were performed using the statistical software R (R core team, 2018) and different packages: vegan (Oksanen et al., 2019), usedist (Bittinger, 2017), factoextra (Kassambara and Mundt, 2017), ggplot2 (Wickham, 2016), dplyr (Wickham et al., 2019) and tidyverse (Wickham, 2017).

3. Results

3.1 Beetle assemblages

A total of 2860 individuals were identified from 313 taxa and 38 families (Table S2). The number of individuals per sample ranged between 58 and 279 (Table S2, Figure 3). In figure 3, depths are according to core 11, which matched best with the master core from 2016 and was used to correlate all other cores to (see Figure S1 – S4). The beetle record was divided into five distinctive zones according to the hierarchical cluster analysis (Figure 4): Zone 1 (930 – 1080 CE), Zone 2 (1080 – 1500 CE), Zone 3 (1500 – 1740 CE), Zone 4 (1740 – 1950 CE) and Zone 5 (1950 CE – present).

Zone 1 (930 – 1080 CE) has a high abundance of aquatic species (21.8 – 24.4%). Especially species living in standing water (e.g. the diving beetle *Hydroporus tristis* and the water scavenger beetle *Anacaena lutescens*) were found but also species living in running water such as *Limnius perrisi*, which feeds on moss from stones in mountain streams (Koch, 1989a; 1989b). Marsh/wetland species (4.4 – 6 %) consist mostly of species in the families Carabidae and Staphylinidae. Species living on or hunting within bank vegetation (6.8 – 10.1 %) consist primarily of *Cyphon* spp. and *Stenus* spp (Koch, 1989b). Species living in rotting materials (Foul/dung; 9 – 12.2 %) primarily consist of a variety of rove beetles, among which many species of the subfamily Aleocharinae. This zone contains a high proportion of species living on deciduous trees (6 – 10 %) which consists almost entirely of the species *Rhynchaenus fagi*, a leaf-mining weevil which colonizes beech trees (Koch, 1989a). The proportion of conifer pests is high in this zone as well (6 – 11.5 %), consisting mostly of the species *Polygraphus poligraphus*, a species which attacks depressed stands of spruce (Pfeffer, 1989). Species living in meadows or glades, such as *Eusphalerum alpinum*, which visit flowers in mountain meadows (Koch, 1989a), are also abundant (5.9 – 10.5 %). *Arpedium quadrum*, a predator in heathlands and alluvial meadows and an indicator of heathland/moorland (Koch, 1989a), is the most abundant species (5.3 %) from the remaining ecological groups.

In Zone 2 (1080 – 1500 CE), common species are *Stenus* spp. (16.1 %), *A. quadrum* (9 %), *Pityogenes chalcographus* (7.5 %), *Pityophthorus pityographus* (5.8 %), *Cyphon* spp. (4.7 %) and *Eusphalerum anale* (3.1 %). The proportion of aquatic beetles declines while marsh/wetland species such as *Trechus* spp. and *Olophrum piceum* increase (Koch, 1989a). Bank species (primarily *Stenus* spp. and *Cyphon* spp.) increase significantly. *Pit. chalcographus* and *P. pityographus* replace *P. poligraphus* as abundant conifer pests (Pfeffer, 1989), but species indicative for shaded woodland, deciduous trees and deadwood species all decline to values below 4 %. Dung species, such as *Aphodius abdominalis* (Koch, 1989b), start to appear in this zone. In the upper part of Zone 2, species living in meadows (such as *Eusphalerum* spp.) increase to 15.3 %.

Zone 3 (1500 – 1740 CE) shows a shift in dominant species: *Cyphon* spp. (8.7 %), *Anotylus tetracarinatus* (6.9 %), *Stenus* spp. (5.5 %), *Pit. chalcographus* (5 %), *Gabrius pennatus* (4.3 %), *Enochrus quadripunctatus* (3.8 %), *A. quadrum* (3.1 %), and *Platystethus arenarius* (3.1 %). *A. tetracarinatus*, *G. pennatus* and *P. arenarius* are found in dung or other rotting substances (Koch, 1989a) while *E. quadripunctatus* is an aquatic generalist (Koch, 1989a). Heathland/moorland species and meadow species decrease in number. Different classes related to woodland do not change significantly in this zone but shaded woodland species such as *Molops piceus* increase slightly to 5.4 % (Koch, 1989a). Dung species (Koch 1989a, 1989b), such as *Aphodius* spp., *Onthophagus* cf. *joannae* and *Sphaeridium lunatum*/*scarabaeoides*, increase to about 5 % of the total beetle assemblage.

Zone 4 (1740 – 1950 CE) contains mainly dominant species connected to the inundated site and its (bank) vegetation: *Cyphon* spp. (18.1 %), *Hydroporus erythrocephalus* (living in a wide range of still water habitats (Koch 1989a; 4.9 %), *Phyllotreta* spp. (4.2 %), *A. lutescens* (3.9 %), *E. quadripunctatus* (3.5 %), *Donacia* spp. (3.5 %) and *Coelostoma orbiculare* (3.4 %). *Cyphon* spp., *Phyllotreta* spp. and *Donacia* spp. feed on bank vegetation

while the other taxa are all aquatic (Koch 1989a, 1989b, 1992). This zone contains a lower amount of species living in running water (0.7 – 2.6 %) as well as lower amounts of conifer pests (2.6 – 4.1 %). Heathland/moorland species decline even further. Sample 6 in this zone (1780 CE) has the highest proportion of dung species (e.g. *Aphodius* spp., *Onthophagus* cf. *joannae* and *Sphaeridium lunatum*/*scarabaeoides*; 7.4 %) of all samples.

Zone 5 (1950 CE – present) has the lowest number of individuals recorded. Aquatic species decline rapidly (down to 5 %) and aquatic beetles living in running water are absent. Marsh species remain between 8.6 – 15.3 % but bank vegetation species decline to levels similar to Zone 2 and 3 (13.8 – 16.7 %). Meadow species and species living in disturbed/arable areas remain consistent. Foul/dung species increase (27.8 %) and dung species are absent between 1970 CE and present. Shaded woodland species such as *Anoplotrupus stercorosus* (Koch, 1989b) increase in the bottom sample of this zone (6.9 %) while conifer pests (e.g. *Pit. chalcographus*) (24%) and species living in deadwood (8 %) peak between 2000 CE – present. Conifer pest *Pit. chalcographus* reaches high values of 13 % of the total assemblage in this zone.

3.2 *Pollen assemblages*

In order to compare the changes in the beetle community to changes in the vegetation, the zonation of the pollen diagram (Figure 5) follows the zonation used for beetle communities. Zone 1 (< 1080 CE) is dominated by pollen from *Picea, Abies* and *Fagus*, with *Pinus* contributing to 10 % of the total pollen sum. Zone 2 (1080 – 1500 CE) consists of two phases: in the first phase there is a maximum of *Abies* and *Picea* pollen, which decline around 1350 CE. Maximum values of *Fagus* pollen occur between 1250 – 1350 CE. Between 1250 – 1500 CE, there are peaks in Poaceae and Cyperaceae, after which *Pinus* pollen increase considerably and *Betula* pollen starts to increase. In contrast, *Fagus* pollen decrease. From 1250 CE, there are notable increases in human indicator taxa, including cultivated plants such as *Secale cereale* and *Triticum avellana* and plants growing on open

mineral soil connected to human settlements such *Plantago lanceolata* (Behre, 1981; Gaillard, 2013). The green alga *Botryococcus neglectus*, indicative for oligotrophic or mesotrophic reservoirs (Komárek and Fott, 1983), increases around 1250 CE. In Zone 3 (1500 – 1740 CE), the peak in *Pinus* pollen is followed by a peak in *Betula* pollen. When the *Betula* pollen peak declines around 1600 CE, *Picea* and Cyperaceae pollen increase, while *Abies* and *Fagus* pollen continue to decrease. *Quercus* and *Corylus* pollen also increase in Zone 3. In Zone 4 (1740 – 1950 CE) *Picea* pollen values reach their second maximum, while *Pinus* pollen gradually increases. Green alga *B. neglectus* decreases to very low values. From 1950 CE (Zone 5), *Pinus* pollen values are as high as in Zone 2. There is also a decrease recorded in Cyperaceae and human indicator pollen taxa.

3.3 Beetle and vegetation diversity

The pollen diversity data extends from 590 CE to present, and the beetle diversity data extends from 930 CE to present (Figure 6). Beetle diversity fluctuates until the highest Shannon diversity occurs around 1500 CE. After this period, beetle diversity declines steadily, with a rapid decline to the lowest Shannon Index values in the most recent samples (from 1950 CE). Pollen diversity fluctuates until a notable increase between 1200 – 1300 CE, followed by a decline until 1500 CE. Pollen diversity then rises into a consecutive steady phase until 1800 CE. After that, pollen diversity drops to minimum values. There is a rapid increase in pollen diversity in the last sample (2004 CE).

3.4 Patterns in beetle diversity

The PCA biplot (Figure 7) shows the 10 beetle taxa that contribute most to the total variance. The first principal component (PC1) explains 34.3 % of the variance whereas the second rotated factors PC2 contribute to 17.9 %. PC1 has the highest loadings from *Cyphon* spp. (bank species, positive loadings), *Stenus* spp. and *A. quadrum* (marsh/wetland and heathland species, respectively, negative loadings). PC2 has the highest loadings of *Pit. chalcographus* (forest pest, positive loadings), *P. poligraphus*, *E. alpinum* and *R. fagi* (forest

pest, meadow species and deciduous tree indicator, respectively, negative loadings). The oldest samples (930 – 1030 CE) are located within the negative portion of PC2; younger samples are located in the positive portion of PC2. The positive portion of PC1 groups the other, with highest values for samples from Zone 4 (1740 – 1900 CE). Samples from Zone 2 (1080 – 1390 CE) and Zone 5 (1950 – 2000 CE) overlap in the PCA biplot.

4. Discussion

4.1. Forest diversity and ecosystem dynamics over the last millennium

A variety of functional beetle communities enabled the reconstruction of past changes in forest composition and biodiversity at Diera Hollow. The high abundances of tree/forest beetle taxa are indicative of a closed forest ecosystem (Robinson, 1991, 2000; Smith et al., 2010), with Norway spruce as the dominant species at the site over the past 1000 years. However, despite relatively consistent dominant forest cover, different beetle communities have succeeded one another, many of which can be related to changes in the local vegetation.

4.1.1. Montane spruce-dominated forest (930 – 1080 CE)

At the beginning of the last millennium, the dominance of forest/tree beetle taxa suggests a predominantly forested environment. Dominant species *R. fagi* and *P. poligraphus* indicate the presence of beech and spruce trees at the site, respectively (Koch, 1992; Pfeffer, 1989). Low abundances of *Pityokteines vorontzowi* indicate the presence of fir trees (Pfeffer, 1989). This is further supported by the pollen record with the presence of *Abies*, *Picea* and *Fagus* pollen. The dominance of dytiscid *H. tristis*, together with an abundance of other diving beetles typically living in peaty pools (Koch, 1989a), suggests that the site was a shallow peat bog. The high abundance of the species *A. quadrum* and *Stenus* spp. suggest that the banks of the peat bog were not densely covered with vegetation (Brundin, 1934; Koch 1989a). Besides, a variety of species populating open areas was present, such as *Eusphalerum* spp. living on flowers in (alpine) meadows (Koch, 1989a), but

393 also *Silpha tristis*, known to feed on carrion (Koch, 1989a), *Limonius aeneoniger* living at
394 forest edges (Laibner, 2000) and various species of flea beetles living on herbs in open
395 areas (e.g. *Chaetocnema* sp.; Koch, 1989b).
396
397 *4.1.2. Increased beetle diversity associated with landscape openness and floristic diversity*
398 *(1080 – 1500 CE)*
399 From around 1250 CE, increasing changes in the species composition of the beetle
400 community indicate landscape openness and an increase in human activity in the region.
401 Beetle diversity appears to be closely linked to floristic diversity in this period, with an
402 increase of taxa living in open landscapes (Figure 4). There is a decline in species living on
403 deadwood (e.g. *Rhizophagus* spp. and *Anobium* sp.) and shaded woodland species (e.g.
404 ground beetle *Pterostichus foveolatus;* Koch, 1989a), suggesting a decline of old-growth
405 forest directly around the forest hollow. *R. fagi* indicates that beech trees remain present but
406 in low numbers. Several taxa living in forest clearings or at open water edges (e.g.
407 *Eusphalerum* spp. and *A. quadrum*) increase to become the dominant taxa and are
408 indicative of landscape openness (Koch, 1989a). Additionally, the presence of *Hydrobius*
409 *fuscipes* indicates that the peat bog was sun-exposed at this time (Fossen et al., 2016). The
410 increased presence of conifer pests; *Pit. chalcographus* and *P. pityographus* between 1430
411 – 1500 CE to 7.5 % of the total beetle assemblage, indicates an abundance of their primary
412 host, Norway spruce (Pfeffer, 1989). However, the pollen record shows lower amounts of
413 *Picea* pollen, suggesting a lower presence of trees. As these bark beetle species are known
414 to colonize thin branches or otherwise young trees, the high presence of these species might
415 have delayed the establishment of mature spruce trees around the site. The presence of *Ips*
416 *acuminatus* and *Pityogenes quadridens* colonizing *Pinus* spp. (Pfeffer, 1989) coincides with
417 an increase in *Pinus* pollen values, suggesting that pine became the dominant tree species
418 at Diera Hollow during this time. The increase of dung beetles living on dung from sheep,
419 cattle and horses (*P. arenarius*, *S. lunatum/ scarabaeoides*, *Onthophagus* cf. *joannae*,
420 *Aphodius mixtus, A. rufipes, A. prodromus;* Koch, 1989b) from 1500 CE suggests an

increase in herding activities. Since both *S. lunatulum/ scarabaeoides* and *O. joannae* prefer horse, cattle or sheep dung (Koch 1989b), it is likely that the increase of dung beetles near the site was caused by the presence of dung from domesticated animals. However, values of dung beetles between 0.4 and 5 % does not suggest pasturing (Robinson, 1991, 2000) and therefore, the site was likely located near routes where cattle and sheep were herded to alpine meadows higher up in the mountains (as hypothesized by Zámečniková, 2008).

4.1.3. Mixed deciduous-coniferous forest with patchy landscape openness (1500 – 1740 CE)

From 1500 CE onward *Cyphon* spp., *Donacia* spp. and *Phyllotreta* spp., all known to live on bank vegetation (Koch, 1989b; 1992), start to increase and become the dominant taxa. An increase in species living on bank vegetation around 1700 CE coincides with a pronounced increase of Cyperaceae, the general food source for these species. The presence of high amounts of *Quercus* pollen suggests an increase in light availability (e.g. Annighöfer et al., 2015). Therefore, it is likely that the landscape openness increased during this time. Low occurrences of the weevil *R. fagi* together with *Fagus* pollen indicate that beech trees remained present near to the site until the end of the 19th century. The presence of *A. stercorosus*, which is found in semi-humid deciduous and mixed forest (Koch, 1989b), confirms the occurrence of deciduous trees around the site, while the presence of conifer pests and species living on conifer trees (e.g. *Polydrusus pallidus*; Koch, 1992) suggests that conifer trees were still present. As dung beetle species continue to occur in the record, the area likely remained impacted by herding activities.

4.1.4. Semi-natural closed forest and decline in beetle diversity (1740 CE – present)

Conifer pests and shaded woodland taxa start to increase from approximately 1800 CE, suggesting that the vicinity of Diera Hollow became dominated by Spruce-Pine forest during this time. This process coincides with human abandonment of the region in the 19th century (Olah et al., 2009). Tatra National park was established in 1949 CE and the effects of forest management such as reforestation in the area are visible in the beetle record with

shaded woodland species increasing and dung beetles no longer present. Although the PCA biplot (Figure 6) shows that samples after 1950 CE are mostly similar to samples between 1080 – 1500 cal CE (Zone 4), many forest beetle species did not reappear, and the original Spruce-Fir-Beech woodland was not restored. The decline in beetle diversity according to the Shannon Index started around 1500 CE and continued before a rapid decrease from 1950 CE. Partitioning of the Shannon Index for different functional groups (see Figure S6) shows that from 1500 CE, the diversity of the beetle assemblages becomes increasingly driven by aquatic taxa. The rapid decline of beetle diversity between 1950 – 2017 CE could be attributed to the infilling or drying out of Diera Hollow, due to the sharp decline of the total amount of aquatic species and the disappearance of species living in running water. Decline of the alga *B. neglectus* from ~1750 CE is also an indication that the pool was decreasing in size (Jankovská and Komárek, 1982). Apart from the slow infilling of the basin, both climatic and anthropogenic changes could have contributed to the drying out of Diera Hollow. During the period 1881–2008, the average annual precipitation in Slovakia decreased by 3.4% (Ministry of Environment of the Slovak Republic, 2005). However, it has been argued that forest plantations can have a negative effect on forest hydrology and affect surface water generation and groundwater recharge, as young forests demand large amounts of water in order to grow (van Dijk and Keenan, 2007).

4.2. Drivers behind changes in the local beetle community and vegetation

Climatic conditions, especially moisture fluctuations, are likely to have played a significant role in the changes in the local vegetation and beetle community. In a study on the Little Ice Age in the High Tatra Mountains (Niedźwiedź, 2004), the highest decrease in temperature and increase in moisture was identified between 1575 – 1676 CE. An increase in pollen from cultivated plants co-occurs with appearances of beetle species living on animal dung from 1250 CE onwards (Figure 2) suggesting farming in the surrounding area. Moreover, an increase in vegetation and beetle diversity associated with landscape openness can be correlated to regional human activity. Even though limited sources are

available, one describes a village called Maklar or Matrei. This was a settlement for livestock herders that was inhabited until 1360 CE (Greb, 1934). From 1400 CE onward, several wars resulted in abandonment of a large part of the region (Cichocki, 2003; Pavercsik, 2003), enabling forest succession (Figure 2, Figure 4). As soon as the region became more stable from ~1500 CE, human recolonization started. Many settlements were founded as mining communities in search for ore and metals, similar to villages in nearby mountain ranges (Jambrich, 2007). A well-recorded example of recolonization in the area itself is Ždiar, located ten kilometres north of Diera Hollow at an altitude of 850 m a.s.l. and founded in the 16th century (Hreško et al., 2015). Socio-economic activities in the village were mainly related to agriculture, farming, logging and charcoal burning, activities which had a pronounced effect on the surrounding landscape (Rączkowska, 2019). As the onset of increased anthropogenic activities around 1500 CE coincides with the changing patterns in beetle diversity compared to vegetation diversity (Figure 6), it is plausible that the decline in local beetle diversity was related to anthropogenic activity. However, as there are no archaeological evidence or historical documents of human settlement in the vicinity of the sampling site, these indications should be considered with caution.

4.3. Implications for nature conservation

This study recorded several saproxylic beetles (European Red List, Nieto and Alexander, 2010), as well as the rare species *Dapsa denticollis* and *Graphoderus zonatus*. The cryptic endomychid *D. denticollis* has been collected in xerothermic grassland and forest steppe habitats in eastern and south-eastern Europe (Franc and Hemala, 2013) and a single individual was found in sample 16 (1080 CE). *G. zonatus* is a large diving beetle which inhabits peaty pools (Koch, 1989a) and was found in samples up to 1840 CE. This species is currently rare in many regions in Europe due to a decline of its habitat (Knoblauch and Gander, 2019). The identified saproxylic species in our study were only identified sporadically and no trend in their occurrence was found. A study by Majzlan (2015) confirms that all identified saproxylic species are currently found within 5 – 10 kilometres from the

505 sampling site Diera Hollow. However, several of the beetle species identified in this study
506 have a mostly unknown ecology and distribution. This especially concerns species with a
507 strictly montane habitat, living in or near peat bogs and marshes (e.g. the leaf beetle
508 *Chrysolina lichenis*; Burakowski et al., 1990). It gives reason to look beyond the
509 standardized red-list saproxylic species (Nieto and Alexander, 2010) and consider the beetle
510 community as a whole. At Diera Hollow, not only beetle taxa indicative for (old-growth) forest
511 changed drastically over the last millennium but also taxa living in the forest hollow. Our
512 findings suggest that the current forest ecosystem and forest beetle species composition
513 remain affected by changes in the landscape that started centuries ago, possibly by the
514 legacy of previous human impact in the area as was found in other European montane
515 regions (e.g. Valsecchi et al., 2010). As argued by Froyd and Willis (2018), the identification
516 of these past baselines and ecological thresholds would contribute to the conservation of
517 insects and other groups of plants and animals in Tatra National Park. Based on our results,
518 we recommend stakeholders of the national park to 1) look further back in time than only a
519 few hundreds of years when considering restoration strategies (e.g. before 1080 CE), 2)
520 include insect diversity in the targets and monitoring of restauration efforts; and 3) include
521 forest hollows and other inundated depressions in conservation strategies for the national
522 park.
523
524 **5. Conclusions**
525 The fossil beetle and pollen record from Diera Hollow suggest that changes in the
526 local beetle and vegetation record were linked to regional changes, most likely driven by
527 anthropogenic activity. The site developed from a semi-closed to closed montane Spruce-
528 Fir-Beech forest at 930 CE, to a more open landscape from 1080 CE onward. Human
529 activities in the region were first recorded in the beetle and pollen record around 1250 CE.
530 From around 1740 CE, human abandonment of the region and subsequently, the
531 establishment of Tatra National Park in 1949 CE resulted in the reestablishment of a closed
532 woodland, but of a different composition than the ancient woodland. While climate was an

533 important driver behind changes in the vegetation and beetle community, anthropogenic
534 activity likely played a significant role in determining the beetle and floristic diversity during
535 the past millennium. Our results suggest that diversity indices such as the Shannon Index
536 can be used to assess ecological thresholds of local flora and fauna through time. Based on
537 our findings, initiatives to restore the original landscape of this region should compare with
538 the situation before 1080 CE. Furthermore, we recommend including beetles and other
539 insect communities in the monitoring of restoration efforts of flora and fauna biodiversity in
540 montane nature reserves as they could contribute to understanding the baselines and
541 ecological thresholds in these regions. Due to the recorded historical presence of rare beetle
542 species connected to peat bogs, we also advise to include mountain peat bogs in studies on
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544
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Figure captions

Figure 1A The study site Diera Hollow, located in the High Tatra Mountains on the Slovak-Polish border. Depicted countries are Slovakia (SK), Czechia (CZ), Poland (PL), Ukraine (UA), Hungary (HU) and Austria (AT). Figure 1B Terrain map after Nikolov et al. (2004), highlighting the area affected by the 2004 windstorm Alžbeta, with the black diamond marking the location of Diera Hollow (49.09885° N, 20.15814° E). Figure 1C shows the sample site during fieldwork in 2017.

Figure 2 Age-depth model based on four radiocarbon dates (Table S1) of master core DIE-16. Calibrated with the IntCal13 curve (Reimer et al., 2013) within a Bayesian age-depth modelling routine 'BACON' (Blaauw and Christen, 2011), which modelled all age information, including the sediment surface, using a Student-t distribution that accounted for scatter and allowed statistical outliers. The Bayesian analysis (Christen and Perez, 2009) partitioned the core into three sections (31.3 cm thick) estimating the accumulation rate for each segment using a Markov Chain Monte Carlo (MCMC) approach. The modelling was constrained by a prior model of sediment accumulation rate (a gamma distribution with mean 20-year cm-1 and shape 1.5) and its variability (memory, a beta distribution with mean 0.2 and shape 20).

Figure 3 Coleoptera functional groups (in percentage of the total number of individuals) from Diera Hollow. According to a D-chord cluster analysis, the section was divided into five zones. Depth and age are presented on the y-axis according to chronology based on a Bacon age-depth model (Figure S1).

Figure 4 Cluster diagram of the 18 samples of Diera Hollow, based on the terrestrial beetle taxa of the assemblages. A square-chord distance matrix was calculated in the program R, after which Ward's minimum variance criterion was used to implement hierarchical clustering.

Figure 5 Percentage pollen diagram from Diera Hollow. The pollen curves show the percentages of each taxa calculated from the terrestrial pollen sum, with trees/shrubs and herb taxa pooled together in the most-left column. Zonation is based on the cluster analysis of the fossil beetle assemblage from the same site.

Figure 6 Shannon diversity index of beetle data and vegetation data (pollen) from Diera Hollow, with added trend lines. Samples run between 590 CE and 2004 CE for the vegetation data and between 930 CE and 2011 CE for the beetle data.

Figure 7 PCA biplot of the beetle data from Diera Hollow. Samples (defined by sample age CE) are divided into five zones according to a D-chord cluster analysis performed on percentage-transformed data. The vectors of the ten species which contribute most to the variance in the data are displayed.

Table S1 Radiocarbon dates from core DIE-16, taken in 2016 from Diera Hollow, High Tatra Mountains, Slovakia.

Table S2 Full species list of identified Coleoptera remains at Diera Hollow.

Figure S1 XRF curves for atmospheric lead (Pb) for the 12 cores taken from Diera Hollow, together with the XRF curve of master core DIE-16.

Figure S2 XRF curves for rubidium (Rb) for the 12 cores taken from Diera Hollow, together with the XRF curve of master core DIE-16.

Figure S3 XRF curves for iron (Fe) for the 12 cores taken from Diera Hollow, together with the XRF curve of master core DIE-16.

Figure S4 Comparison of the atmospheric lead (Pb) signals of core Die11 with the master core Die2016 which was radiocarbon dated at four different depths (Table S1, black asterixis; three depicted). The cores were divided into five zones (red lines) according to the atmospheric lead signal and, primarily for the lower part of the cores, according to iron (Fe) and rubidium (Rb) concentrations. Cores Die1-Die10 and Die12 were correlated to Die11 in a similar way by wiggle-matching. Zones were divided in three or four samples, where possible in accordance with their geochemical signals. The lowest two zones were often less straightforward to distinguish and evenly divided in four samples. This resulted in 18 samples of unequal size. Depths of the upper and lower boundaries of each sample (red and grey bars in core Die11) were extrapolated to the depths of the master core and then compared to the age-depth model.

from the master core (See figure S1) in order to determine the upper and lower age boundary of each sample.

Figure S5 Shannon Index partitioning for the different beetle ecological groups.